Mathematical Biology



Stoichiometric theory in optimal foraging strategy

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Received: 12 January 2024 / Revised: 30 July 2024 / Accepted: 19 October 2024 © The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2024

Abstract

Understanding how organisms make choices about what to eat is a fascinating puzzle explored in this study, which employs stoichiometric modeling and optimal foraging principles. The research delves into the intricate balance of nutrient intake with foraging strategies, investigating quality and quantity-based food selection through mathematical models. The stoichiometric models in this study, encompassing producers and a grazer, unveils the dynamics of decision-making processes, introducing fixed and variable energetic foraging costs. Analysis reveals cell quota-dependent predation behaviors, elucidating biological phenomena such as "compensatory foraging behaviors" and the "stoichiometric extinction effect". The Marginal Value Theorem quantifies food selection, highlighting the profitability of prey items and emphasizing its role in optimizing foraging strategies in predator–prey dynamics. The environmental factors like light and nutrient availability prove pivotal in shaping optimal foraging strategies, with numerical results from a multi-species model contributing to a comprehensive understanding of the intricate interplay between organisms and their environment.

Keywords Ecological stoichiometry · Predator–prey · Compensatory foraging behaviors · Stoichiometric extinction effect

Mathematics Subject Classification $~34C23\cdot 34D20\cdot 37G15\cdot 92B05$

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1 Introduction

Ecological stoichiometry delves into the study of energy (carbon) and elemental (such as phosphorus and nitrogen) balances within ecological interactions, recognizing that all organisms are fundamentally composed of these elements. The variation in their relative abundance across different species and trophic levels greatly influences food web dynamics. In the realm of producer-consumer interactions, ecological stoichiometry mandates a dual focus on both food quantity and quality. The Optimal Foraging Theory, which seeks to predict behavioral strategies that optimize fitness, traditionally prioritizes energy intake or food quantity as a measure of fitness (Pyke 1977; Pyke et al. 1977). However, the maximization of energy intake does not always correspond with an organism's overall fitness, considering their complex chemical makeup (Simpson et al. 2004). This discrepancy arises due to the elemental mismatches between grazers and their food sources, which significantly affect growth and reproduction (Sterner and Elser 2002). Consuming nutritionally imbalanced diets presents a range of tradeoffs, requiring a fine balance between foraging efforts, nutrient deficit compensations, and the management of surplus nutrient intake. Recent studies indicate that animals adapt their foraging strategies based on the nutritional value of their food, underscoring a shift in focus from quantity to quality of food (Simpson et al. 2004). This shift highlights the essential link between ecological stoichiometry and foraging behaviors, pointing towards a complex understanding of ecological interactions. Additional studies reinforcing these concepts in Andersen et al. (2004), the authors explored the implications of nutrient ratios in aquatic ecosystems and examined the effects of nutrient availability on primary production. The authors in Cross et al. (2005) contributed by analyzing how variable stoichiometry influences consumer-resource dynamics, while the results in Hessen et al. (2013) provided insights into the ecological and evolutionary consequences of stoichiometric principles. Together, these studies enrich our understanding of the complex interplay between the nutritional makeup of organisms and their foraging strategies in the natural world.

To investigate the effects of stoichiometry-dependent foraging strategies under varying nutrient conditions, we developed producer-grazer models within the Ecological Stoichiometry framework (Sterner and Elser 2002). These models intricately balance the quantitative and qualitative aspects of food resources, emphasizing the role of chemical elements and their ratios in trophic interactions. A significant advancement in this field was the adaptation of the Rosenzweig-MacArthur model by Andersen (1997), who incorporated stoichiometric constraints to account for nutrient-deficient growth. This adaptation, which modified both the producer's growth rate and the grazer's efficiency, has profoundly impacted system dynamics and stability (Andersen 1997; Andersen et al. 2004). Building on this, the LKE model (attributed to Loladze, Kuang, and Elser) by Loladze et al. (2000) introduced a complex perspective on the chemical heterogeneity of both producers and grazers, especially focusing on carbon (C) and phosphorus (P) ratios. By allowing variability in the P:C ratio of the producer, this model infused the crucial aspect of food quality into ecological modeling. These developments align with the principles of Optimal Foraging Theory, as proposed by Pyke (1977), which emphasizes the role of food quality in foraging decisions. Further exploring this intersection, Suzuki-Ohno et al. (2012) and Elser et al. (2016)

have demonstrated the significance of stoichiometry in shaping foraging strategies and consumer-resource dynamics. The integration of stoichiometric principles with foraging behavior has revealed complex dynamics in ecological models, including the existence of multiple equilibria, bistability, and deterministic extinction scenarios. These models are now beginning to unveil quantitatively new and fascinating dynamics in autotroph-herbivore interactions, marked by a deeper understanding of the stoichiometric underpinnings of ecological systems.

In ecological modeling, particularly regarding grazer ingestion rates in stoichiometric contexts, the prevalent approach has been to employ various Holling type functional responses, focusing primarily on producer quantity rather than quality. This traditional method is well-documented in foundational works such as Holling (1965, 1966) and extended in studies (Loladze et al. 2000; Wang et al. 2008; Peace et al. 2013, 2014; Peace 2015). However, more recent sophisticated computer simulations have integrated stoichiometric foraging strategies, acknowledging the influence of varying ingestion, assimilation, and metabolism rates affected by factors like gut passage time and temperature, as shown in studies in Darchambeau (2005), Mitra and Flynn (2007), Acheampong et al. (2014). A significant advancement in this field is Suzuki's model of compensatory feeding, which integrates optimal foraging rates into a grazer functional response, particularly addressing the limited ability of filter feeders like Daphnia to distinguish between different food qualities Suzuki-Ohno et al. (2012). Our research builds upon this foundation by presenting an optimal foraging model that factors in the energetic cost of foraging in relation to the nutritional composition of producers, parameterized with empirical data from Elser et al. (2016). Furthermore, we have developed a non-foraging model by modifying the functional form of the grazer ingestion rate and introducing a fixed energetic cost for foraging efforts into the stoichiometric producer-grazer model as proposed in Wang et al. (2008).

Our research contributes a unique perspective to the field of ecological modeling by integrating biological stoichiometry with food selection strategies. This approach sets our work apart from previous studies like Miller et al. (2004) and Andersen (1997). Miller et al. investigated a two-patch consumer-resource system with constant available nutrients, whereas our model operates under a closed system with dynamic nutrient interactions. Additionally, Andersen (1997) model, despite sharing similarities in terms of including two producers and a consumer with stoichiometric considerations, differs significantly from ours. Andersen's model is set in an open nutrient system (chemostats) and does not include competition or self-limitation among producers. Further enriching this field, authors in Peace and Wang (2019) investigated compensatory foraging in stoichiometric producer-grazer models, providing valuable insights into the complexities of such systems. Our work aligns with this trajectory but also expands upon it by integrating biological stoichiometry with food selection strategies through combining rigorous mathematical analysis with extensive numerical simulations. Our model adeptly navigates the intricate relationship between foraging strategies and population dynamics, offering enhanced insights into ecological systems. It stands out by bridging the gap between stoichiometry and food selection, thus filling a crucial knowledge void in ecological understanding.

The structure of this paper is outlined as follows: Sect. 2 delves into the formulation of the general model, laying the groundwork for the subsequent analyses. Section 3 focuses on exploring two distinct models, each involving two producers and one consumer. In Sect. 4, we broaden our examination to include a multi-species model, extending the scope of our investigation. Finally, the paper concludes with a comprehensive discussion in Sect. 5, where we synthesize our findings and reflect on their implications.

2 Model construction

In this section, we formulate a general foraging model for preys $(x_i, i = 1, 2, ..., n)$ and a predator (y) in an aquatic environment. It is well documented that the elemental composition of pery varies widely when compared to that of aquatic herbivores (Sterner and Elser 2002). Additionally, predator has high nutrient demands, they are often limited by the quantity of mineral elements in their food, rather than the amount of food or energy available (Sterner and Hessen 1994). To incorporate such stoichiometric constraints, we assume the prey has variable P:C ratios Q_i and the predator has a constant P:C ratio θ . The amount of free P in the environment is denoted as R. The model assumes that the grazer foraging behavior depends on available producer quantity and quality through Holling type II functional response and also incorporates the cost of feeding effort.

$$\frac{dx_i}{dt} = \underbrace{b_i(x_i, Q_i)x_i}_{\text{gain from growth}} - \underbrace{f_i(x_i, Q_i)y}_{\text{loss from predation}}, \\ \frac{dy}{dt} = \sum_i e(Q_i) f_i(x_i, Q_i)y - \sum_i \xi_i(Q_i)y - \underbrace{dyy}_{\text{loss from death}}, \\ \frac{dQ_i}{dt} = \underbrace{\rho_i(Q_i, R)}_{\text{uptake from environment}} - \underbrace{b_i(x_i, Q_i)Q_i}_{\text{loss due to growth}}, \\ \frac{dR}{dt} = -\sum_i \rho_i(Q_i, R)x_i + \theta(\sum_i \xi_i(Q_i) + d_y)y \\ \underbrace{Q_i}_{\text{uptake from prey}} = -\sum_i \rho_i(Q_i) f_i(x_i, Q_i)y_i, \\ \underbrace{Q_i}_{\text{uptake from prey}} = 1, 2, ..., n. \end{cases}$$
(1)

Now we will describe the general functions of the model (1) as follows: *Prey growth rate* The growth rate of i-th prey follows Droop cell quota growth:

$$b_i(x_i, Q_i) = r_i \min\left[1 - \frac{x_i}{K_i}, 1 - \frac{q_i}{Q_i}\right],$$

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where r_i is the intrinsic growth rate and q_i is the minimum P:C ratio for prey *i*.

Prey P:C uptake rate Prey uptakes P and C following the below uptake function:

$$\rho_i(Q_i, R) = \left[\frac{\rho_i^M R}{\nu_i + R}\right] \left[\frac{Q_i^M - Q_i}{Q_i^M - q_i}\right],$$

where ρ_i^M is the prey maximum P:C uptake rate and v_i is the half saturation constant. The maximum P:C ratio for prey *i* is Q_i^M and its minimum P:C ratio is q_i .

Predator conversion efficiency

$$e(Q_i) = e_i \min\left\{1, \frac{Q_i}{\theta}\right\},\$$

where e_i is the maximum predator conversion efficiency and θ is the predator constant P:C ratio.

Predator functional response The predator's functional response $f_i(x_i, Q_i)$ for can be denoted as

$$f(x_i, Q_i) = \frac{\mu \xi_i(Q_i) x_i y}{1 + \sum_i \mu \xi_i(Q_i) \tau_i x_i},$$

where ξ_i is the maximum ingestion rate, τ_i is the handling time, and μ is the amount of water cleared per mg C invested to generate energy for filtering behavior. This function can be parameterized using the data provided by Schatz and McCauley (2007). The estimated maximum ingestion rates from the slopes of fitted exponential decay functions for each treatment and parameterized ξ_i as a quadratic function of the algal P:C given as

$$\xi_i(Q_i) = a_i Q_i^2 + b_i Q_i + c_i; \quad b_i^2 - 4a_i c_i < 0.$$

The above relation and the positive constants a_i , b_i , and c_i are also used in Peace and Wang (2019). Similar to earlier models developed within the Ecological Stoichiometry framework, such as those by Andersen et al. (2004) and Loladze et al. (2000), our models incorporate a nonsmooth minimum function in the expressions for growth rate. This approach is inspired by Justin Leibig's Law of the Minimum, which posits that an organism's growth is constrained by the scarcest resource in comparison to its needs (Sterner and Elser 2002). In this context, we hypothesize that growth rates are constrained either by carbon (C) or phosphorus (P), leading to the application of minimum functions with two inputs in our model's growth expressions, as incorporated in model (1).

Now we will consider some general biological assumptions to reduce the model. First, we consider the total amount of phosphorus in the system $P = R + \sum_{i} Q_{i}x_{i} + \theta y$ is conserved. According to the model (1), we get

$$\frac{dP}{dt} = \frac{dR}{dt} + \sum_{i} Q_i \frac{dx_i}{dt} + \sum_{i} x_i \frac{dQ_i}{dt} + \theta \frac{dy}{dt} = 0.$$

In other words, our model ecosystem is a closed system with respect to nutrients where the free nutrients can be expressed as $R = P - \sum_{i} Q_{i}x_{i} - \theta y$. Now we can explicitly measure the total free nutrients in the environment and get rid of the differential equation for change in environmental resources over time. As in Peace and Wang (2019), additional assumptions on the efficiency of the producer nutrient uptake can further reduce the models. We also assume the producer is extremely efficient at nutrient uptake and allows unbounded uptake which removes the upper bound on the producer P:C ratio. The dynamics of the nutrients in the producer, Q_i , and the media, R, are much faster than the population growth dynamics of x_i and y. For sufficiently fast nutrient processes under quasi-steady-state assumptions, the model (1) takes the following reduced form:

$$\frac{dx_i}{dt} = b_i(x_i, Q_i)x_i - f_i(x_i, Q_i)y,
\frac{dy}{dt} = \sum_i e(Q_i)f_i(x_i, Q_i)y - \sum_i \xi_i(Q_i)y - d_yy,
i = 1, 2, ..., n,$$
(2)

where

$$P = \sum_{i} Q_{i} x_{i} + \theta y.$$
(3)

The equation (3) could not explicitly determine the P:C ratio (Q_i) in prey over time. We will use an assumption during exponential growth (fast nutrient uptake) to find out the condition for the P:C in preys. During exponential growth, quotas (Q_i) quickly reach equilibrium while nutrients are still abundant. According to Sterner and Elser (2002), under exponential growth, the nutrients are saturating, and prey stoichiometry remains consistent regardless of which nutrient is limiting, implying that phytoplankton "are what they eat." Applying this condition to two prey in Klausmeier et al. (2004), which we extend to multiple prey, we can express the condition as:

$$\frac{Q_j}{Q_i} = \frac{q_j}{q_i}, \quad j = 1, 2, \dots, (i-1).$$
(4)

The equations from (2) to (4) present the general reduced optimal foraging model. All the parameter descriptions and values for the model (2) are given in the following Table 1.

3 The two-producer, one-consumer model

In this section, we will discuss the two-producer and one-consumer models. First, we present a base model (Sect. 3.1) where foraging behavior depends on available producer quantity, then we develop an optimal foraging model (Sect. 3.2) where foraging behavior depends on available producer quantity and quality.

Parameter list		
Symbol	Description	Value
Р	Total phosphorus (mg P/L)	0.01-0.08
K _i	Producer carrying capacity (mg C/L)	0-2.5
r _i	Maximal growth rate of producer (/d)	1.1-1.3
d	Grazer loss rate (/d)	0.12
θ	Grazer constant P:C	0.03
q_i	Producer minimal P:C (mg P/mg C)	0.003-0.004
ei	Maximal production efficiency	0.7 - 0.9
μ	Water cleared/mg C invested to generate filtering energy (L/mg C)	700
$ au_i$	Handling time (d)	1.2-1.3
ξ _i	Feeding cost, constant for base model (mg P/mg C/d)	0.003-0.004
$\xi_i(Q_i) =$	Feeding cost, function for optimal foraging model	$a_i = 5.17$
	$\xi_i(Q_i) = a_i Q_i^2 + b_i Q_i + c_i$	$b_i = -0.31$
		$c_i = 0.007$

Table 1 Description of variables and parameters of the model (2) taken from Peace and Wang (2019)

3.1 The base model

In our base model, we explore the first two trophic levels of an aquatic food chain, comprising two primary producers, Phytoplankton (x_1) and Periphyton (x_2) , along with the grazer Daphnia (y). Given that Daphnia typically face limitations due to the mineral content in their food rather than the sheer quantity available, we focus on the nutrient dynamics, particularly the phosphorus-to-carbon (P:C) ratio. The producers are assumed to have a variable P:C ratio, Q_i , while the grazer maintains a constant P:C ratio, θ . The model also tracks the amount of free phosphorus (P) in the environment, denoted as resource R, which is represented by the equation $R = P - Q_1 x_1 - Q_2 x_2 - \theta y$. The base model for two prey and one predator takes the following form:



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$$\underbrace{e_{2}\min\left\{1,\frac{Q_{2}}{\theta}\right\}\frac{\mu\xi_{2}x_{2}y}{1+\mu\xi_{1}\tau_{1}x_{1}+\mu\xi_{2}\tau_{2}x_{2}}}_{\text{Growth for Periphyton}} -\underbrace{(\xi_{1}+\xi_{2})y}_{\text{Cost of feeding effort}} -\underbrace{d_{y}y}_{\text{loss from death}}.$$
(5)

With similar assumptions as discussed in the Sect. 2 using Eqs. (3) and (4), we get following cell quota equations

$$Q_1 = \alpha Q_2, \quad Q_2 = \frac{P - \theta y}{\alpha x_1 + x_2}, \quad \alpha = \frac{q_1}{q_2}.$$

The boundedness and positive invariance of the solutions of (5) are assured by the following theorem, which demonstrates that system (5) is biologically well-defined. The proof of the theorem is given in Appendix A.1.

Theorem 1 Solutions with initial conditions in the set

$$\Omega = \{ (x_1, x_2, y) : 0 < x_1 < k_1, 0 < x_2 < k_2, 0 < y < P/\theta, q_1x_1 + q_2x_2 + \theta y < P \}$$

will remain in Ω for all forward time, where $k_i = \min\{K_i, \frac{P}{q_i}\}, i = 1, 2$.

In order to find the dynamics of the base model (5), we rewrite the base model in the following form:

$$\frac{dx_1}{dt} = x_1 F(x_1, x_2, y), \quad \frac{dx_2}{dt} = x_2 G(x_1, x_2, y), \quad \frac{dy}{dt} = y H(x_1, x_2, y),$$

where

$$F(x_1, x_2, y) = \begin{cases} r_1 \left[1 - \frac{x_1}{K_1} \right] - \mu \xi_1 y \Delta(x_1, x_2), & \text{if } 1 - \frac{x_1}{K_1} \le 1 - \frac{q_1}{Q_1}; \\ r_1 \left[1 - \frac{q_1}{Q_1} \right] - \mu \xi_1 y \Delta(x_1, x_2), & \text{if } 1 - \frac{x_1}{K_1} > 1 - \frac{q_1}{Q_1}; \end{cases}$$
$$G(x_1, x_2, y) = \begin{cases} r_2 \left[1 - \frac{x_2}{K_2} \right] - \mu \xi_2 y \Delta(x_1, x_2), & \text{if } 1 - \frac{x_2}{K_2} \le 1 - \frac{q_2}{Q_2}; \\ r_2 \left[1 - \frac{q_2}{Q_2} \right] - \mu \xi_2 y \Delta(x_1, x_2), & \text{if } 1 - \frac{x_2}{K_2} > 1 - \frac{q_2}{Q_2}; \end{cases}$$

 $H(x_1, x_2, y)$

$$=\begin{cases} (e_{1}\mu\xi_{1}x_{1} + e_{2}\mu\xi_{2}x_{2})\Delta(x_{1}, x_{2}) - \xi_{1} - \xi_{2} - d, & \text{if } 1 \leq \frac{Q_{1}}{\theta} \text{ and } 1 \leq \frac{Q_{2}}{\theta}; \\ (e_{1}\mu\xi_{1}x_{1} + e_{2}\frac{Q_{2}}{\theta}\mu\xi_{2}x_{2})\Delta(x_{1}, x_{2}) - \xi_{1} - \xi_{2} - d, & \text{if } 1 \leq \frac{Q_{1}}{\theta} \text{ and } 1 > \frac{Q_{2}}{\theta}; \\ (e_{1}\frac{Q_{1}}{\theta}\mu\xi_{1}x_{1} + e_{2}\mu\xi_{2}x_{2})\Delta(x_{1}, x_{2}) - \xi_{1} - \xi_{2} - d, & \text{if } 1 > \frac{Q_{1}}{\theta} \text{ and } 1 \leq \frac{Q_{2}}{\theta}; \\ (e_{1}\frac{Q_{1}}{\theta}\mu\xi_{1}x_{1} + e_{2}\frac{Q_{2}}{\theta}\mu\xi_{2}x_{2})\Delta(x_{1}, x_{2}) - \xi_{1} - \xi_{2} - d, & \text{if } 1 > \frac{Q_{1}}{\theta} \text{ and } 1 \leq \frac{Q_{2}}{\theta}; \end{cases}$$

where $\Delta(x_1, x_2) = (1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2)^{-1}$. Our base stoichiometric model (5) has four consumer-free equilibria that always exist and the local stability of these equilibria is given in the following theorem.

Theorem 2 Let us denote four consumer-free equilibria as (i) $E_{000} = (0, 0, 0)$, (ii) $E_{100} = (k_1, 0, 0)$, (iii) $E_{010} = (0, k_2, 0)$, and (iv) $E_{110} = (k_1, k_2, 0)$. The (i)-(iii) consumer-free equilibria are unstable but the $E_{110} = (k_1, k_2, 0)$ is locally stable if $H(k_1, k_2, 0) < 0$.

The proofs of local stability of equilibria are given in the Appendix A.2. Since the origin, $E_{000} = (0, 0, 0)$, is always a saddle-node, there cannot be total extinction of the system for positive initial conditions $x_1 > 0$, $x_2 > 0$, and y > 0. Furthermore, in the absence of the consumer, both prey will survive regardless of how poor their quality may be. Our next theorem extends the global existence of consumer-free equilibria.

Theorem 3 If
$$\xi_1 + \xi_2 + d_y \ge e_1 \min\left\{\mu\xi_1k_1, \frac{1}{\tau_1}, \frac{\mu\xi_1k_1Q_1}{\theta}\right\} + e_2 \min\left\{\mu\xi_2k_2, \frac{1}{\tau_2}, \frac{\mu\xi_2k_2Q_2}{\theta}\right\}$$
, then
$$\lim_{t \to \infty} (x_1(t), x_2(t), y(t)) = (k_1, k_2, 0)$$

where $k_i = \min\{K_i, \frac{P}{q_i}\}$ with i = 1, 2.

The proof of this theorem can be found in Appendix A.2. This result states that the consumer goes extinct if it cannot acquire sufficient quality from both producers at a sufficiently high rate. We can get a sharp result even if predator choose absolutely good quality of food $(Q_i > \theta)$ under predation. The following result exhibits that even good quality of food does not help predator to exist if the cost of feeding is higher.

Theorem 4 Suppose
$$Q_i > \theta$$
 with $i = 1, 2$. Let $\delta = \max_{(x_1, x_2) \in [0, k_1] \times [0, k_2]} = \left[\frac{e_1 \mu \xi_1 x_1 + e_2 \mu \xi_2 x_2}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} - (\xi_1 + \xi_2 + d_y)\right]$. If $\bar{\delta} < 0$, then
$$\lim_{t \to \infty} y(t) = 0.$$

The proof of this theorem can be found in Appendix A.2. We also characterize the factors which are related to the growth of the predator population. From the predator equation

$$\frac{dy}{dt} = e_1 \min\left\{1, \frac{Q_1}{\theta}\right\} \frac{\mu \xi_1 x_1}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2}$$

$$f_1 = \text{Growth Contributed by prey 1}$$

$$+ \underbrace{e_2 \min\left\{1, \frac{Q_2}{\theta}\right\} \frac{\mu \xi_2 x_2}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2}}_{f_2 = \text{Growth Contributed prey 2}} y - (\xi_1 + \xi_2)y - dy.$$

Here, if $f_1 > f_2$, growth is contributed mainly by prey 1, and otherwise prey 2. To show the importance of food quality and food quantity on predator population dynamics,

we introduce the indicator for prey quality as Qual_i which defined as

$$\operatorname{Qual}_i = \min\left\{1, \frac{Q_i}{\theta}\right\}, \quad i = 1, 2,$$

and the indicator for prey quantity as Quant_i which defined as

$$Quant_i = \frac{Actual \text{ per unit consumption}}{Maximum Consumption} = \frac{\tau_i x_i}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2}, \quad i = 1, 2.$$

For prey 1, when $\text{Qual}_1 < 1$, the quality of prey 1 is bad. When $\text{Qual}_1 = 1$, the quality of prey 1 is good. To quantify the relative importance of food quality and food quantity, we define an index below to identify which is the more limiting factor for predator growth. That is

$$\text{Index}_i = \frac{\text{Qual}_i}{\text{Quant}_i}, \quad i = 1, \ 2,$$

when $Index_1 < 1$, growth is limited by the quality of prey 1, otherwise the quantity of prey 1. A similar index is also used for prey 2 as well. To quantify food selection we use the marginal value theorem (MVT) that usually describes the behavior of an optimally foraging individual in a system (Stephens and Krebs 2019). Predators have to decide whether to eat the prey they find or look for another more profitable source of prey. They do this by considering the handling time (how long it takes to prepare the prey for eating), and energy they would gain. To determine the profitability in this model, the value of energy the predator will receive should be divided by the handling time. The prey with the higher value is more profitable. The profitability formula for ith prey is

Profitability_i =
$$\frac{\text{Energy Content of Prey}_i \text{ (per time)}}{\text{Handling Time}_i} = \frac{f_i(x_i, Q_i)}{\tau_i}, \quad i = 1, 2.$$
 (6)

Now, we will discuss the numerical results related to base model (5). We investigate how light intensity (K_i) influences the dynamics, particularly under varying nutrient levels (α) in the prey. This study is crucial as the consumer's choice, represented by Daphnia in our model, is heavily influenced by its strict phosphorus-to-carbon ratio (θ) which, in turn, depends on the quality of the food (Q_i). The numerical technique involves using Matlab to solve the model (5) with biologically reasonable values of the studied parameters. To determine the cycle amplitude for each parameter value, we select the maxima and minima after the fluctuations stabilize to the limit cycle. The unstable steady state is computed using the "fsolve" command. By setting the right-hand sides of the model to zero and applying "fsolve," we obtain the internal steady state for each parameter value. Computing the cycle period for each studied parameter value is more challenging. We simulate for a sufficiently long time to ensure fluctuations stabilize to the limit cycle, then calculate the shifts between two consecutive maxima and between two consecutive minima, both of which provide the cycle period.



Fig. 1 Bifurcation diagram of the Base model (5) under different light-dependent carrying capacity (K_1) for $\alpha = 1$ (homogeneous nutrient level) and $K_2 = 1.4$, P = 0.05

We consider two scenarios: one where nutrient conditions are uniformly distributed in the environment, and another where they are not. To model these, different values of α are used; $\alpha = 1$ signifies equal nutrient levels in both types of prey, while $\alpha \neq 1$ indicates varied nutrient levels. In Fig. 1, we plot bifurcation diagrams for the system to observe the impact of light intensity on system dynamics, starting with the scenario where both types of prey have the same nutrient level ($\alpha = 1$).

The Fig. 1 demonstrates that in the range of $0 < K_1 < 1.5$, a limit cycle forms around the interior equilibrium, indicating periodic oscillations in the populations of both the consumer (Daphnia) and the producers. At very low light levels (K_1) , Phytoplankton growth is predominantly light-limited, whereas at higher light intensities, it becomes nutrient-limited. As depicted in Fig. 2, under lower light conditions (smaller K_1 values), Daphnia's growth primarily relies on prev 2 (Periphyton) but shifts to dependence on prey 1 (Phytoplankton) as light availability increases. Numerically we have found that the predator (Daphnia) transitions to selecting prey 1 (Phytoplankton) when K_1 is greater than 1.25. Additionally, as shown in Fig. 1, the upper-density limit of the system increases with K_1 , eventually leading to the disappearance of the limit cycle and the establishment of an interior equilibrium when K_1 surpasses 1.5. Concurrently, the predator density gradually decreases with increasing K_1 , which can be attributed to stoichiometric principles: higher K_1 results in lower quality food, thereby reducing Daphnia's overall growth. The next phase of our analysis involves examining the scenario where the nutrient levels in both prey are different, with $\alpha = 1.2$, as shown in Fig. 3.

In Fig. 3, the growth dynamics of the predator, Daphnia, and the prey species (Phytoplankton and Periphyton) mirror those observed in Fig. 1. The Appendix A.3 provides time series diagrams for various light intensities (K_1). Notably, this model reveals variations in Daphnia's selectivity under different nutrient levels, as examined in Fig. 4. This figure presents a phase diagram depicting the system's dynamics in terms of the carrying capacities of phytoplankton (K_1) and periphyton (K_2). The regions are colorcoded and marked with symbols to indicate whether the predator's foraging strategy is based on the quality or quantity of the prey. Blue and red squares and asterisks denote regions where the predator targets phytoplankton, with squares representing exclusive focus and asterisks indicating dominance. Green and magenta squares and asterisks





Fig. 2 Dynamics of the base model (5) under different light-dependent carrying capacity (K_1) of Phytoplankton (x_1) for $\alpha = 1$ (homogeneous nutrient level)

represent regions where the predator focuses on periphyton. Cyan squares mark areas where the predator adopts a mixed foraging strategy. Each point on the graph shows the mean prey density over 2000 days, highlighting how different carrying capacities influence the predator's behavior and the resulting prey dynamics. The figure also illustrates how nutrient content affects the predator's food choice. Under uniform nutrient conditions, as in Fig.4a, Daphnia selects food based on both quality and quantity uniformly. However, under varying nutrient conditions, as shown in Figs.4b and c, Daphnia's strategy changes. At low and high light intensities, the predator prioritizes food based on quality and quantity due to the abundance of choices. At intermediate



Fig. 3 Bifurcation diagram of the base model (5) under different light-dependent carrying capacity (K_1) for $\alpha = 1.2$ (non-homogeneous nutrient level) and $K_2 = 1.4$, P = 0.05

light levels, Daphnia adopts a mixed-food strategy to optimize growth, demonstrating flexible and strategic selection in response to environmental changes.

In the base model (5), the cost of the predator's feeding effort, which is expressed in carbon (C) units, is denoted as $\sum_i \xi_i y$. This cost reflects the reduction in predator density due to the energy expended in feeding. The model also delves into the survival dynamics of the consumer, as discussed in the context of Theorem 3 and Theorem 4. Figure 5 showcases these dynamics by illustrating the cost of feeding effort under various conditions. It becomes evident that a consumer's likelihood of survival is significantly higher when the quality of food is good, as shown in Fig. 5a, compared to scenarios where the food quality is poor, as depicted in Fig. 5b and c. This is particularly noticeable in low-light conditions where Daphnia have access to higher quality food. Additionally, the model suggests that in adverse environmental conditions, such as those presented in Fig. 5b with P = 0.08 and Fig. 5c with P = 0.05, the consumer's chances of survival are further reduced. These findings underline the critical role of environmental factors and food quality in the survival and thriving of consumers like Daphnia in aquatic ecosystems.

3.2 The foraging model

The Optimal Foraging Theory posits that animals forage in a way that maximizes their fitness, which is an indicator of their reproductive success and adaptability to their environment, thereby influencing natural selection. This theory suggests that foraging behaviors are fine-tuned by natural selection to optimize fitness, considering the forager's capacity to locate, capture, and process food. In our discussion, we extend this concept to a stoichiometric foraging model for both producers and consumers. This model closely resembles our base model (5) but introduces key modifications: the grazing response of the consumer (Daphnia) and its feeding effort are now dependent on the quality of available food. Building upon the assumptions outlined in Sect. 2, we present the foraging model incorporating two producers and one consumer, where these dynamics are intricately linked to the nutritional quality and availability of the resources in the ecosystem.



Fig. 4 Daphnia food selection for the base model varying light-dependent carrying capacities (K_1) and (K_2) under homogeneous nutrient level (**a** $\alpha = 1$), and non-homogeneous nutrient level (**b** $\alpha = 1.2$, **c** $\alpha = 0.8$)

$$\frac{dx_1}{dt} = r_1 x_1 \min\left[1 - \frac{x_1}{K_1}, 1 - \frac{q_1}{Q_1}\right] - f_1(x_1, x_2, y, Q_1),
\frac{dx_2}{dt} = r_2 x_2 \min\left[1 - \frac{x_2}{K_2}, 1 - \frac{q_2}{Q_2}\right] - f_2(x_1, x_2, y, Q_2),
\frac{dy}{dt} = e_1 \min\left\{1, \frac{Q_1}{\theta}\right\} f_1(x_1, x_2, y, Q_1) + e_2 \min\left\{1, \frac{Q_2}{\theta}\right\} f_2(x_1, x_2, y, Q_2)
-\xi_1(Q_1)y - \xi_2(Q_2)y - d_y y,$$
(7)



Fig. 5 Survival of consumer dynamics (y) for base model (5) under different nutrient conditions, with $\alpha = 1$, **a** P = 0.05, $K_1 = 0.5$, $K_2 = 0.5$, with $\alpha = 1.2$, **b** P = 0.08, $K_1 = 1.5$, $K_2 = 1.25$, and **c** P = 0.05, $K_1 = 1.5$, $K_2 = 1.25$

where

$$f_1(x_1, x_2, y, Q_1) = \frac{\mu \xi_1(Q_1) x_1 y}{1 + \mu \xi_1(Q_1) \tau_1 x_1 + \mu \xi_2(Q_2) \tau_2 x_2},$$

$$f_2(x_1, x_2, y, Q_2) = \frac{\mu \xi_2(Q_2) x_2 y}{1 + \mu \xi_1(Q_1) \tau_1 x_1 + \mu \xi_2(Q_2) \tau_2 x_2},$$

$$Q_1 = \alpha Q_2, \quad Q_2 = \frac{P - \theta y}{\alpha x_1 + x_2}, \quad \text{and} \quad \xi_i(Q_i) = a_i Q_i^2 + b_i Q_i + c_i, \quad i = 1, 2.$$

The analytical methods used for the base model have been similarly applied to the foraging model, with detailed results presented in appendices **B**.1 and **B**.2. A notable outcome of this analysis is the emergence of additional dynamics under intermediate



Fig. 6 Bifurcation diagram of the foraging model (7) under different light-dependent carrying capacity (K_1) for $\alpha = 1$ (homogeneous nutrient level) and $K_2 = 1.4$, P = 0.05

nutrient conditions (specifically in the range 0.02 < P < 0.03). In this scenario, the optimal foraging model develops two new interior equilibria, leading to a state of bistability. This means that the system has two separate stable interior equilibria, as detailed in the Sect. Appendix B.3. Such a finding is significant as it illustrates the complex interplay between nutrient availability and the foraging strategies of organisms, potentially leading to multiple stable states in the ecosystem under certain conditions.

In our numerical analysis of the foraging model, we conduct a series of simulations using biologically realistic parameter values sourced from existing literature, as outlined in Table 1. These simulations are particularly focused on varying specific parameters to understand their impact on the ecosystem. By adjusting the light intensity parameter (K_1), we can explore its influence on the population dynamics of Periphyton and Phytoplankton. Additionally, by altering the levels of total phosphate (P), we can observe the resulting changes in population densities. This approach allows us to identify critical thresholds at which light and nutrients switch roles between being abundant resources to becoming limiting factors in the ecosystem. Such insights are crucial for understanding the delicate balance of factors that govern the health and sustainability of aquatic ecosystems.

The bifurcation diagram Fig. 7 for the foraging model shows that within the light intensity range of $0 < K_1 \le 2.5$, the system displays periodic cycles and stable coexistence equilibria as K_1 increases. This behavior is similar to what was observed in the base model (5). When comparing these results with the bifurcation diagrams of the base model (as seen in Fig. 1), it's evident that periodicity in the foraging model occurs over a broader range of K_1 values. Specifically, in Fig. 6, when the light intensity is within the range $0 < K_1 < 1.8$, a limit cycle forms around the interior equilibrium, leading to periodic oscillations of both consumer and producer populations. In scenarios of very low light availability (K_1), Phytoplankton's growth is primarily constrained by light, while at high light levels, growth becomes nutrient-limited. As K_1 increases, the upper density limit also rises, resulting in the disappearance of the limit cycle and the emergence of an interior equilibrium once K_1 exceeds 1.8. Additionally, Fig. 7 indicates that under lower light conditions (small K_1), growth predominantly comes from prey 2, but shifts to rely more on prey 1 as K_1 increases. Also, the predator (Daphnia) in the foraging model starts to select prey 1 (Phytoplankton) when K_1 is



Fig. 7 Dynamics of the foraging system (7) under different light-dependent carrying capacity (K_1) of Phytoplankton (x_1) for $\alpha = 1$ (homogeneous nutrient level)

greater than 1.5, which is higher than the switch point in the base model, indicating a different response to environmental changes in the foraging context.

The foraging model reveals almost similar trends in Daphnia's food selectivity as observed in the base model, particularly when the nutrient levels are uniform ($\alpha = 1$). This is evident when comparing Figs. 4b and 8a, where the predator consistently selects food based on a combination of quality and quantity. However, under varied nutrient conditions, as shown in Fig. 8b and c, the predator's food selection behavior diverges significantly, especially under varying light intensities. In conditions of low and high light, Daphnia in the foraging model strictly prioritizes food based on both



Fig. 8 Daphnia food selection for foraging model varying light-dependent carrying capacities (K_1) and (K_2) under homogeneous nutrient level (**a** $\alpha = 1$), and non-homogeneous nutrient level (**b** $\alpha = 1.2$, **c** $\alpha = 0.8$)

its quality and quantity, similar to the base model. But notably, at intermediate light intensities, the predator in the foraging model adopts a more flexible, mixed-food strategy, compared to the base model. This adaptive approach in the foraging model is more pronounced, allowing the predator to optimize its growth by selectively choosing food based on quality from other resources. This finding underscores the predator's enhanced ability in the foraging model to spend more effort in searching for higher quality food, which is a significant adaptation for ensuring better survival and fitness in varying environmental conditions.

In the context of the foraging model (7), the Marginal Value Theorem (MVT) plays a pivotal role in understanding and quantifying the food selection behavior of optimally foraging predators. The MVT essentially guides predators in deciding whether to consume prey 1 (x_1) or prey 2 (x_2), based on an assessment of the profitability of each prey type. This profitability is calculated by taking into account factors such as handling time, which refers to the duration needed to capture, subdue, and prepare



Fig. 9 Profitability of food selection for Daphnia using Marginal value theorem. Here $\alpha = 1.2, K_1 = 1.75$ $K_2 = 1.25, P = 0.05$

the prey for consumption, as well as the energy gain from consuming the prey. In our model, the profitability of each prey item is determined by dividing its energy value by the handling time required (as indicated in equation (6)). The prey that offers a higher profitability ratio is considered more advantageous for the predator to consume. This approach, as outlined in Fig. 9c, is crucial in demonstrating how the MVT can be applied to optimize foraging strategies. It showcases a strategic decisionmaking process in predators, balancing the energy expenditure involved in handling prey against the nutritional gain, thereby maximizing their efficiency and survival in a dynamic ecological environment.

The Fig. 10 offers valuable insights into how a consumer's grazing behavior adapts in response to varying foraging strategies and nutrient imbalances. Central to this understanding is the Optimal Foraging Theory, a cost-benefit model that advocates for an optimal foraging approach aimed at minimizing energy expenditure and maximizing energy intake. This theory is particularly relevant in explaining the predator's behavior in the foraging model. A key observation from these figures is the extended limit cycle interval of the predator in the foraging model compared to the base model. In Fig. 10a, the black curve in the base model shows a shorter limit cycle interval than



Fig. 10 Flexibility of grazing by the consumer under different nutrient conditions

the colored graphs representing the foraging model. In the foraging model, higher nutrient variation leads to this extended limit cycle interval. This delay in reaching a stable state highlights the dynamic and flexible food selection strategies under different nutrient conditions. The results from the foraging model suggest that these adaptive strategies are crucial for the predator's survival, especially in environments with fluctuating prey densities. The consumer exhibits remarkable adaptability in its grazing habits, particularly when faced with a variety of nutrient conditions. This adaptability is evident in the predator's ability to consume a mixed diet, efficiently responding to nutrient level fluctuations in the environment. Energy enrichment further enhances this adaptability, as increased foraging for quality resources allows the predator to access higher-quality foods and sustain more flexible grazing patterns (see Fig. 10b and c). Both Fig. 10b and c demonstrate that under homogeneous nutrient conditions ($\alpha = 1$) and favorable environmental conditions (total phosphorus P = 0.07), predators select higher quality foods, which reduces the quantity of available food. Figure 10c also shows that if nutrient conditions vary among foods, predators select a mixed variation of quality foods. Such flexibility in food selection and consumption patterns ensures the predator's sustained survival and highlights the intricate interplay between ecological factors, energy enrichment, and animal behavior in natural ecosystems.

4 Multi-species foraging model

The Optimal Foraging Theory, functioning as a cost-benefit model, posits that there is an optimal method for foraging that aims to minimize energy expenditure while maximizing energy gain. In this section, we will discuss a special case of model (2) for the multi-species model by considering five different prey and one predator. In addition, we will consider the same assumption to derive model (2) that the total amount of phosphorus in the system is conserved, which gives $P - \sum_{i=1}^{5} Q_i x_i = 0$.

For the system involving five prey and a predator, the corresponding set of differential equations is as follows:

$$\frac{dx_i}{dt} = r_i \min\left[1 - \frac{x_i}{K_i}, 1 - \frac{q_i}{Q_i}\right] - \frac{\mu\xi_i(Q_i)x_iy}{1 + \sum_i \mu\xi_i(Q_i)\tau_i x_i},
\frac{dy}{dt} = \sum_i e_i \min\left\{1, \frac{Q_i}{\theta}\right\} \frac{\mu\xi_i(Q_i)x_iy}{1 + \sum_i \mu\xi_i(Q_i)\tau_i x_i} - \sum_i \xi_i(Q_i)y - dy,
\xi_i(Q_i) = a_i Q_i^2 + b_i Q_i + c_i; \quad b_i^2 - 4a_i c_i < 0, \ i = 1, 2, \dots, 5.$$
(8)

Furthermore, the model incorporates an optimal uptake assumption. When nutrients are abundant, the stoichiometry of the prey remains consistent regardless of the limiting nutrient. This assumption is represented by the condition $\frac{Q_j}{Q_i} = \alpha_j$ for j = 1, 2, 3, 4. In cases where all α_j values are identical, the scenario is referred to as a homogeneous nutrient condition, indicating that the consumer (predator) is surrounded by prey with similar nutrient (P:C) ratios. Conversely, when the α values differ, it represents a non-homogeneous nutrient condition, suggesting variability in the nutrient ratios among different prey species. This distinction is crucial for understanding the predator's foraging behavior and survival strategy within such a multi-species ecological system.

In our numerical analysis of the multi-species model (8), we conduct simulations using biologically realistic parameters, as detailed in Table 1. These simulations are designed to explore the effects of varying nutrient conditions on predator population dynamics, with a specific focus on the parameter α_i . This parameter is pivotal in understanding how different P:C (phosphorus-to-carbon) ratios in prey species influence the foraging behavior and population dynamics of a predator, in this case, Daphnia, which is typical in aquatic ecosystems. The Fig. 11 illustrates scenarios under homogeneous nutrient conditions, where all prey species have the same P:C ratios. This uniformity in nutrient content allows us to isolate and examine the effects of other variables, such as different growth rates (r_i) and light intensities (K_i) , on the ecosystem. The subfigures a and b in Fig. 11 will likely demonstrate the impact of varying growth rates on the population dynamics under low light intensity, while Fig. 11c and d will show how changes in high light intensity affect the predator and prey populations under same growth as previous. This approach provides a comprehensive understanding of the ecological interactions in a multi-species system, particularly highlighting how consistent nutrient levels across different prey species can influence the overall dynamics of the predator-prey relationship.



Fig. 11 Dynamics of the system (8) with respect to different growth rates (r_i) and light intensities (K_i) under the same nutrient condition $(\alpha_i = 1)$. The growth rates are set as $r_1 = 1.6$, $r_2 = 1.5$, $r_3 = 1.4$, $r_4 = 1.3$, and $r_5 = 1.2$ for all figures. For Figs. **a** and **b**, the light intensities are $K_1 = 0.5$, $K_2 = 0.58$, $K_3 = 0.45$, $K_4 = 0.53$, and $K_5 = 0.52$. For Figs. **c** and **d**, the light intensities are $K_1 = 0.69$, $K_2 = 0.72$, $K_3 = 0.70$, $K_4 = 0.73$, and $K_5 = 0.74$

Figure 11 effectively demonstrates how, under homogeneous nutrient conditions (where all α_i are equal to 1), the growth of the predator Daphnia is primarily influenced by the availability and abundance of its prey. In such a scenario, Daphnia tends to favor prey with higher growth rates, as their abundance makes them more accessible and, therefore, a more significant contributor to its diet. This preference is exemplified in Fig. 11c and d, where prey x_2 demonstrates the highest growth rate, making it a key food source for Daphnia. Conversely, Fig. 12 explores the dynamics under non-homogeneous nutrient conditions, where P:C ratios vary among the prey species. This variability introduces a more complex dimension to Daphnia's food selection behavior. Unlike the homogeneous scenario, Daphnia now has to employ a more strategic approach to foraging, considering not only the prey's abundance and growth rates but also their differing nutrient profiles. For instance, in Fig. 12c and d, even though prey x_4 has a high population density, the high P:C ratio of prey x_1 makes it a more critical contributor to Daphnia's growth. This scenario underscores Daphnia's adaptability and strategic foraging in response to the varying nutritional quality of its food sources. These observations from Figs. 11 and 12 highlight the intricate and dynamic interactions within predator-prey relationships in ecological systems. They emphasize how predators like Daphnia must continually adapt their foraging strategies



Fig. 12 Dynamics of the system (8) with respect to different growth rates (r_i) and light intensities (K_i) under varying nutrient conditions (α_i) . For **a** and **b**, the nutrient conditions are $\alpha_1 = 1.1$, $\alpha_2 = 1.4$, $\alpha_3 = 1.2$, and $\alpha_4 = 0.8$, with growth rates $r_1 = 1.6$, $r_2 = 1.5$, $r_3 = 1.4$, $r_4 = 1.3$, and $r_5 = 1.2$, and light intensities $K_1 = 0.5$, $K_2 = 0.58$, $K_3 = 0.45$, $K_4 = 0.53$, and $K_5 = 0.52$. For **c** and **d**, the nutrient conditions are $\alpha_1 = 1$, $\alpha_2 = 1.2$, $\alpha_3 = 1.4$, and $\alpha_4 = 0.8$, with growth rates $r_1 = 1.2$, $r_2 = 1.5$, $r_3 = 1.4$, $r_4 = 1.3$, and $r_5 = 1.5$, and light intensities $K_1 = 0.69$, $K_2 = 0.72$, $K_3 = 0.7$, $K_4 = 0.73$, and $K_5 = 0.74$

to the ever-changing environmental conditions and the nutritional availability of their prey to optimize their growth and survival.

5 Discussion

The optimal foraging behaviors of grazers are contingent upon both the availability of food and stoichiometric constraints. The base model (5) represents a stoichiometric producer-grazer model employing a Holling type II functional response. This model incorporates the carbon cost of feeding efforts, as proposed by Suzuki-Ohno et al. (2012). Expanding upon this, the optimal foraging model (7) introduces the assumption that feeding effort is quadratically related to food quality, aligning with empirical observations by Elser et al. (2016). By comparing these two models, we aim to glean insights into the conditions under which optimal foraging behaviors prove beneficial for grazers.

In environments characterized by intermediate phosphorus levels and varying light intensities, grazers modeled under the base framework seem to outperform those in the optimal foraging model. However, simulations shown in Fig. 10 indicate that grazers in the optimal foraging model benefit from increased flexibility in their grazing strategies. This adaptability allows them to alter their feeding habits in response to the changing environmental dynamics, which is critical for their survival. Such flexibility might involve varying the types of plants they consume, modifying their feeding times, or switching between different foraging strategies to adapt to diverse ecological conditions. The presence of multiple attractors in these models also highlights that the ecological outcomes in stoichiometric and nutrient-diverse environments are heavily influenced by the initial conditions of both resources and consumers. Depending on these initial conditions, the system can either reach an equilibrium with the consumer population becoming extinct or find a balance where both consumer and resource populations coexist, as depicted in Fig. 17.

Studying oscillatory dynamics vis-à-vis Hopf bifurcation in the model is important for readers such as ecologists or biologists to gain insights into foraging strategies. As our study focuses on food selection, understanding the limit cycle is crucial. During the cyclic period, the predator switches between different foods (see Figs. 2 and 7), which helps elucidate the conditions under which stable populations become oscillatory. This knowledge provides valuable information on how predators adapt their foraging strategies in response to changes in prey availability and environmental conditions, contributing to a deeper understanding of predator–prey dynamics.

In the equilibrium case of our ecological models, we have the opportunity to visually compare and analyze the per capita growth rates of grazers in both the base and optimal foraging models, with a focus on how these rates function in relation to the quality of food sources (Q_i), while keeping the quantity of food sources (x_i) constant. The base model becomes

$$\frac{dy/dt}{y} = e_1 \min\left\{1, \frac{Q_1}{\theta}\right\} f_1(x_1, x_2) + e_2 \min\left\{1, \frac{Q_2}{\theta}\right\} f_2(x_1, x_2) - \xi_1 - \xi_2 - d,$$

and the optimal foraging model becomes

$$\frac{dy/dt}{y} = e_1 \min\left\{1, \frac{Q_1}{\theta}\right\} f_1(x_1, x_2, Q_1) + e_2 \min\left\{1, \frac{Q_2}{\theta}\right\} f_2(x_1, x_2, Q_2) -\xi_1(Q_1) - \xi_2(Q_2) - d.$$

In Fig. 13a, we see graphical representations depicting the variations in the per capita growth rates of grazers derived above under different food quality values (Q_1 and Q_2) in the context of equilibrium conditions. These surfaces highlight the potential benefits of compensatory feeding behaviors, particularly in scenarios where the food nutrient content is at an intermediate level, as indicated by the blue region in Fig. 13b. Notably, the height differences between the two surfaces (one representing the base model and the other the optimal foraging model) in Fig. 13 are often marginal. This is particularly evident when the fitness derived from the base model (shown in red) surpasses that from the optimal foraging model (shown in blue), suggesting that the advantages of varying foraging strategies might be limited, especially in light of potential uncertainties in parameter values. It's important to recognize that these surfaces represent the system



Fig. 13 Per capital growth rates of the grazer population for the base model (red) and the foraging model (blue) under non-homogeneous nutrient condition $\alpha = 1.2$ (color figure online)

dynamics strictly under equilibrium conditions. For scenarios where the dynamics are oscillatory, bifurcation diagrams would offer a more comprehensive understanding of the system's behavior.

The Fig. 14 illustrates the mean density of two prey species $(x_1 \text{ and } x_2)$ over a time of 2000 days for each combination of carrying capacities $(K_1 \text{ and } K_2)$ for two different models: the base model (in red) and the foraging model (in blue). The left graph shows that the mean density of prey species x_1 is higher in the foraging model compared to the base model, particularly at higher values of K_1 and K_2 . Similarly, the right graph indicates that the foraging model supports a higher mean density of prey species x_2 than the base model across the same range of carrying capacities. This intriguing dynamic benefits the prey species, as the process of consumer predation involves selectively capturing individual prey. As a result of this increased overall prey density, a dilution effect is observed: with more prey available, the probability of any single prey being targeted and consumed by a predator diminishes. This effect serves to enhance the overall survival and fitness of the prey population. Essentially, the presence of a larger number of prey creates a sort of "safety in numbers", providing individual prey with a better chance of evading predation, thereby contributing to the stability and sustainability of the prey population within the ecosystem.

Through analysis and simulation, our model demonstrates that diverse and intriguing dynamics are possible in a model that considers both stoichiometry and nutrient heterogeneity. By including the more realistic assumption that an organism's growth depends on both the quality and quantity of the food it consumes, we can develop models that contain new population dynamics. Consideration of ecological stoichiometry and consumer dispersal in heterogeneous habitats can bring new insight to the study of biodiversity and stability in ecosystems. For example, we can examine under what conditions consumers consume food from resources with different stoichiometric properties to provide enhanced or reduced opportunities for sustaining species. Stoichiometry may provide another analytical framework; one which provides a deterministic mechanism for extinction. In addition, permitting a consumer species to disperse between food selection can sometimes rescue the consumer from extinc-



Fig. 14 Mean prey density under consumer predation

tion. But, in Sect. 3, we have seen that when the resource quality can determine the growth of the consumer, the consumer can go extinct even with dispersal. When prey of different quality, permitting consumers to consume still can lead to the extinction of a resource species (by Theorem 3). This was observed in our "stoichiometric extinction effect". However, we can enrich our discussion of this phenomenon with stoichiometry where a rich food can increase the overall population of consumers, and subsequent dispersal of the consumer to the rich food can depress the growth of the consumer. Additionally, the models were parameterized using values derived from empirical observations, and several parameter values were adopted from prior studies (refer to Table 1). However, the absence of long-term datasets capturing population dynamics alongside corresponding measurements of varying stoichiometric ratios poses a challenge for model validation. Although forthcoming datasets will contribute to validating these models, the analyses presented in this study offer insights into the qualitative dynamics that may emerge as light and phosphorus levels vary, rather than providing precise quantitative predictions. It is important to note that incorporating spatial variation in food quality can add complexity to population dynamics. A study by Schatz and McCauley (2007) investigated how Daphnia responded under a spatial gradient of algal phosphorus-to-carbon (P:C) ratios while keeping algal densities constant. The findings revealed that Daphnia adjusted their ingestion rates and efficiently located regions with high-quality food.

While we have conducted some study on the parameters Q_1 , Q_2 , K_1 , and K_2 , our primary focus has been on identifying foraging strategies based on the quality and quantity of foods. We acknowledge that a detailed sensitivity analysis of how the outcomes are affected by changes in these parameters is limited in this study. Understanding the sensitivity of the model to these parameters could provide deeper insights into which factors are most critical for foraging strategies and extinction

effects. Future research could benefit from a comprehensive sensitivity analysis to identify key parameters that significantly influence the system's dynamics. This would enhance our understanding of the robustness and applicability of the model under various environmental conditions and parameter uncertainties.

Appendix A Base model analysis

Appendix A.1 Boundedness and positivity

The proof of boundedness and positive invariance of the solutions of (5) (Theorem 1) is given below.

Proof We will prove the theorem by contradiction. Suppose that the solution to the model S(t) starts inside our region and there exists some t_1 such that $S(t_1) \in \partial \Omega$, then it must either stay on the boundary or turn back into the interior of Ω . To consider the

following cases using $\hat{y} = \max_{t \in [0,t_1]} y(t) < \frac{P}{\theta}, \ \hat{x_1} = \max_{t \in [0,t_1]} x_1(t) < \min\{K_1, \frac{P}{q_1}\}, \text{ and } \hat{x_2} = \max_{t \in [0,t_1]} x_2(t) < \min\{K_2, \frac{P}{q_2}\}.$

Case 1

$$x_1(t_1) = 0$$
. Define $f(x_1) = \frac{\mu\xi_1 x_1}{1 + \mu\xi_1\tau_1 x_1 + \mu\xi_2\tau_2 \hat{x}_2}$ and let $\hat{f} = f'(0) = \lim_{x_1 \to 0} \frac{f(x_1)}{x_1}$. Then we have

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \min\left[1 - \frac{x_1}{K_1}, 1 - \frac{q_1}{Q_1}\right] - \frac{\mu \xi_1 x_1 y}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} \\ &\geq r_1 x_1 \min\left[1 - \frac{x_1}{K_1}, 1 - \frac{q_1}{Q_1}\right] - \frac{\mu \xi_1 x_1 \hat{y}}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 \hat{x}_2} \\ &\geq -\hat{f} x_1 \hat{y} = -\phi x_1, \end{aligned}$$

which implies that $x_1(t_1) \ge x_1(0) \exp^{-\phi t_1} > 0$, where ϕ is a constant. This contradicts $x_1(t_1) = 0$ and proves that $S(t_1)$ does not reach this boundary.

Case 2 $x_2(t_1) = 0$. Define $f(x_2) = \frac{\mu \xi_1 x_2}{1 + \mu \xi_1 \tau_1 \hat{x}_1 + \mu \xi_2 \tau_2 x_2}$ and let $\hat{f} = f'(0) = \lim_{x_2 \to 0} \frac{f(x_2)}{x_2}$. Then we have

$$\begin{aligned} \frac{dx_2}{dt} &= r_2 x_2 \min\left[1 - \frac{x_2}{K_2}, 1 - \frac{q_2}{Q_2}\right] \frac{\mu \xi_2 x_2 y}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} \\ &\geq r_2 x_2 \min\left[1 - \frac{x_2}{K_2}, 1 - \frac{q_2}{Q_2}\right] - \frac{\mu \xi_2 x_2 \hat{y}}{1 + \mu \xi_1 \tau_1 \hat{x}_1 + \mu \xi_2 \tau_2 x_2} \\ &\geq -\hat{f} x_2 \hat{y} = -\phi x_2, \end{aligned}$$

which implies that $x_2(t_1) \ge x_2(0) \exp^{-\phi t_1} > 0$, where ϕ is a constant. This contradicts $x_2(t_1) = 0$ and proves that $S(t_1)$ does not reach this boundary.

Case 3 $y(t_1) = 0$, note that $\forall t \in [0, t_1]$ we have

$$\frac{dy}{dt} = e_1 \min\left\{1, \frac{Q_1}{\theta}\right\} \frac{\mu \xi_1 x_1 y}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} \\ + e_2 \min\left\{1, \frac{Q_2}{\theta}\right\} \frac{\mu \xi_2 x_2 y}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} \\ - \xi_1 y - \xi_2 y - dy \\ \ge -\xi_1 y - \xi_2 y - dy = -\alpha y,$$

which implies that $y(t_1) \ge y(0) \exp^{-\alpha t_1} > 0$, where α is a constant. This contradicts $y(t_1) = 0$ and proves that $S(t_1)$ does not reach this boundary.

Case 4 At $t = t_1$, we have $q_1x_1(t_1) + q_2x_2(t_1) + \theta y(t_1) = P$, we can consider

$$r_1 x_1(t_1) \left[1 - \frac{x_1(t_1)}{\min\{K_1, \frac{P - x_2 Q_2 - \theta y}{q_1}\}} \right] \le r_1 x_1(t_1) \left[1 - \frac{x_1(t_1)}{\frac{P - x_2 q_2 - \theta y}{q_1}} \right] = 0,$$

similarly

$$r_{2}x_{2}(t_{1})\left[1-\frac{x_{2}(t_{1})}{\min\{K_{2},\frac{P-x_{1}Q_{1}-\theta y}{q_{2}}\}}\right] \leq r_{2}x_{2}(t_{1})\left[1-\frac{x_{2}(t_{1})}{\frac{P-x_{1}q_{1}-\theta y}{q_{2}}}\right]=0,$$

we have $0 < e_1, e_2 < 1$, and $\min(\theta, q_i) \le q_i < 1$, that gives

$$\begin{aligned} \frac{d(q_1x_1 + q_2x_2 + \theta y)}{dt}|_{t=t_1} \\ &= q_1x_1' + q_2x_2' + \theta y'|_{t=t_1} \\ &= e_1 \left[\min\left\{\theta, q_1\right\} - 1\right] \frac{\mu\xi_1 x_1 y}{1 + \mu\xi_1 \tau_1 x_1 + \mu\xi_2 \tau_2 x_2} \\ &+ e_2 \left[\min\left\{\theta, q_2\right\} - 1\right] \frac{\mu\xi_2 x_2 y}{1 + \mu\xi_1 \tau_1 x_1 + \mu\xi_2 \tau_2 x_2} - \theta(\xi_1 + \xi_2 + d)y \le 0. \end{aligned}$$

Therefore, $S(t_1)$ cannot cross this boundary.

Case 5 $x_1(t_1) = k_1 = \min\{K_1, \frac{P}{q_1}\}$. Since the phosphorus in the phytoplankton cannot exceed the total phosphorus in the system we must have

$$x_1Q_1 \leq P$$
.

That gives

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \min\left[1 - \frac{x_1}{K_1}, 1 - \frac{q_1}{Q_1}\right] - \frac{\mu \xi_1 x_1 y}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} \\ &\leq r_1 x_1 \left[1 - \frac{x_1}{\min\{K_1, \frac{x_1 Q_1}{q_1}\}}\right] \\ &\leq r_1 x_1 \left[1 - \frac{x_1}{\min\{K_1, \frac{P}{q_1}\}}\right]. \end{aligned}$$

By standard comparison argument, $x_1(t_1) = k_1$, therefore S(t) cannot cross the boundary $x_1 = k_1$. A similar type of argument can be used for the case $x_2(t_1) = k_2 = \min\{K_2, \frac{P}{q_2}\}$.

All possibilities that $S(t_1)$ touches or crosses the boundary of Ω are excluded. Therefore, Ω set is positive invariant with respect to System (5). We thus claim that each solution of System (5) with initial condition $S(0) \in \Omega$ stays in Ω for any $t \ge 0$.

Appendix A.2 Dynamics of the base model

The following is the proof of the Theorem 2.

Proof To determine the local stability of equilibria, we calculate the Jacobian matrix of the base model

$$J(x_1, x_2, y) = \begin{pmatrix} F + x_1 F_{x_1}(x_1, x_2, y) & x_1 F_{x_2}(x_1, x_2, y) & x_1 F_y(x_1, x_2, y) \\ x_2 G_{x_1}(x_1, x_2, y) & G + x_2 G_{x_2}(x_1, x_2, y) & x_2 G_y(x_1, x_2, y) \\ y H_{x_1}(x_1, x_2, y) & y H_{x_2}(x_1, x_2, y) & H + y H_y(x_1, x_2, y) \end{pmatrix}.$$

$$F_{x_1} = \begin{cases} -\frac{r_1}{K_1} - \mu^2 \xi_1^2 \tau_1 y \Delta^2, & \text{if } 1 - \frac{x_1}{K_1} \le 1 - \frac{q_1}{Q_1}; \\ -r_1 \left(\frac{q_1}{Q_1}\right)_{x_1} - \mu^2 \xi_1^2 \tau_1 y \Delta^2, & \text{if } 1 - \frac{x_1}{K_1} > 1 - \frac{q_1}{Q_1}; \end{cases}$$

$$F_{x_2} = \begin{cases} -\mu^2 \xi_1 \xi_2 \tau_2 y \Delta^2, & \text{if } 1 - \frac{x_1}{K_1} \le 1 - \frac{q_1}{Q_1}; \\ -r_1 \left(\frac{q_1}{Q_1}\right)_{x_2} - \mu^2 \xi_1 \xi_2 \tau_2 y \Delta^2, & \text{if } 1 - \frac{x_1}{K_1} > 1 - \frac{q_1}{Q_1}; \end{cases}$$

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$$F_{y} = \begin{cases} -\mu\xi_{1}\Delta, & \text{if } 1 - \frac{x_{1}}{K_{1}} \leq 1 - \frac{q_{1}}{Q_{1}}; \\ -r_{1}\left(\frac{q_{1}}{Q_{1}}\right)_{y} - \mu\xi_{1}\Delta, & \text{if } 1 - \frac{x_{1}}{K_{1}} > 1 - \frac{q_{1}}{Q_{1}}; \end{cases}$$

$$G_{x_{1}} = \begin{cases} -\mu^{2}\xi_{2}\xi_{1}\tau_{1}y\Delta^{2}, & \text{if } 1 - \frac{x_{2}}{K_{2}} \leq 1 - \frac{q_{2}}{Q_{2}}; \\ -r_{2}\left(\frac{q_{2}}{Q_{2}}\right)_{x_{1}} - \mu^{2}\xi_{2}\xi_{1}\tau_{1}y\Delta^{2}, & \text{if } 1 - \frac{x_{2}}{K_{2}} > 1 - \frac{q_{2}}{Q_{2}}; \end{cases}$$

$$G_{x_{2}} = \begin{cases} -\frac{r_{2}}{K_{2}} - \mu^{2}\xi_{2}^{2}\tau_{2}y\Delta^{2}, & \text{if } 1 - \frac{x_{2}}{K_{2}} \leq 1 - \frac{q_{2}}{Q_{2}}; \\ -r_{2}\left(\frac{q_{2}}{Q_{2}}\right)_{x_{2}} - \mu^{2}\xi_{2}^{2}\tau_{2}y\Delta^{2}, & \text{if } 1 - \frac{x_{2}}{K_{2}} > 1 - \frac{q_{2}}{Q_{2}}; \end{cases}$$

$$G_{y} = \begin{cases} -\mu\xi_{2}\Delta, & \text{if } 1 - \frac{x_{2}}{K_{2}} \leq 1 - \frac{q_{2}}{Q_{2}}; \\ -r_{2}\left(\frac{q_{2}}{Q_{2}}\right)_{y} - \mu\xi_{2}\Delta, & \text{if } 1 - \frac{x_{2}}{K_{2}} > 1 - \frac{q_{2}}{Q_{2}}; \end{cases}$$

also,

$$\begin{pmatrix} \frac{q_1}{Q1} \end{pmatrix}_{x_1} = \frac{q_1}{P - \theta y}, \ \begin{pmatrix} \frac{q_1}{Q1} \end{pmatrix}_{x_2} = \frac{q_1}{\alpha (P - \theta y)}, \ \begin{pmatrix} \frac{q_2}{Q2} \end{pmatrix}_{x_1} = \frac{q_2 \alpha}{P - \theta y}, \ \begin{pmatrix} \frac{q_2}{Q2} \end{pmatrix}_{x_2} = \frac{q_2}{P - \theta y}.$$

At the E_{000} , the Jacobian matrix takes the form

$$J(E_{000}) = \begin{pmatrix} r_1 & 0 & 0 \\ 0 & r_2 & 0 \\ 0 & 0 & -\xi_1 - \xi_2 - d \end{pmatrix}.$$

The eigenvalues come with a different sign. That gives E_0 is always unstable. This implies that a complete collapse of the system is impossible.

At E_{100} , the Jacobian matrix is

$$J(E_{100}) = \begin{pmatrix} k_1 F_{x_1}(k_1, 0, 0) \ k_1 F_{x_2}(k_1, 0, 0) \ k_1 F_{y}(k_1, 0, 0) \\ 0 \ G(k_1, 0, 0) \ 0 \\ 0 \ 0 \ H(k_1, 0, 0) \end{pmatrix}$$
$$= \begin{pmatrix} -* & * \\ 0 \ r_2 \ 0 \\ 0 \ 0 \ H(k_1, 0, 0) \end{pmatrix}.$$

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The eigenvalues come with a different sign, which does not matter on the sign of $H(k_1, 0, 0)$. That gives E_{100} unstable as well.

At E_{010} , the Jacobian matrix is

$$\begin{split} I(E_{010}) &= \begin{pmatrix} F(0, k_2, 0) & 0 & 0 \\ k_2 G_{x_1}(0, k_2, 0) & k_2 G_{x_2}(0, k_2, 0) & k_2 G_y(0, k_2, 0) \\ 0 & 0 & H(0, k_2, 0) \end{pmatrix} \\ &= \begin{pmatrix} r_1 & 0 & 0 \\ * & - & * \\ 0 & 0 & H(0, k_2, 0) \end{pmatrix}. \end{split}$$

We get E_{010} is unstable.

At E_{110} , biologically the ratio between total phosphorus and minimum P:C ratio $\left(\frac{P}{q_I}\right)$ is way too high than the carrying capacity (K_i) . That gives $k_1 = \min\{K_1, \frac{P}{q_1}\} = K_1$ and $k_2 = \min\{K_2, \frac{P}{q_2}\} = K_2$ and our equilibria becomes $E_{110} = (K_1, K_2, 0)$. Then the Jacobian matrix becomes

$$J(E_{110}) = \begin{pmatrix} k_1 F_{x_1}(k_1, k_2, 0) & k_1 F_{x_2}(k_1, k_2, 0) & k_1 F_y(k_1, k_2, 0) \\ k_2 G_{x_1}(k_1, k_2, 0) & k_2 G_{x_2}(k_1, k_2, 0) & k_2 G_y(k_1, k_2, 0) \\ 0 & 0 & H(k_1, k_2, 0) \end{pmatrix}$$
$$= \begin{pmatrix} -0 & * \\ 0 & - & * \\ 0 & 0 & H(k_1, k_2, 0) \end{pmatrix}.$$

The stability of $E_{110} = (K_1, K_2, 0)$ depends on the condition of $H(k_1, k_2, 0) < 0$.

The proof of Theorem 3 is given below.

Proof From consumer (y) equation, we get

$$\begin{aligned} \frac{dy}{dt} &= -y \bigg[\xi_1 + \xi_2 + d - e_1 \min \left\{ 1, \frac{Q_1}{\theta} \right\} \frac{\mu \xi_1 x_1}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} \\ &+ e_2 \min \left\{ 1, \frac{Q_2}{\theta} \right\} \frac{\mu \xi_2 x_2}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} \bigg] \\ &\leq -y \bigg[\xi_1 + \xi_2 + d - e_1 \min \left\{ 1, \frac{Q_1}{\theta} \right\} \frac{\mu \xi_1 x_1}{1 + \mu \xi_1 \tau_1 x_1} + e_2 \min \left\{ 1, \frac{Q_2}{\theta} \right\} \frac{\mu \xi_2 x_2}{1 + \mu \xi_2 \tau_2 x_2} \bigg] \\ &\leq -y \bigg[\xi_1 + \xi_2 + d - e_1 \min \left\{ \frac{\mu \xi_1 x_1}{1 + \mu \xi_1 \tau_1 x_1}, \frac{Q_1}{\theta} \frac{\mu \xi_1 x_1}{1 + \mu \xi_1 \tau_1 x_1} \right\} \end{aligned}$$

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$$+ e_{2} \min\left\{\frac{\mu\xi_{2}x_{2}}{1 + \mu\xi_{2}\tau_{2}x_{2}}, \frac{Q_{2}}{\theta} \frac{\mu\xi_{2}x_{2}}{1 + \mu\xi_{2}\tau_{2}x_{2}}\right\}\right]$$

$$\leq -y\left[\xi_{1} + \xi_{2} + d - e_{1} \min\left\{1, \frac{1}{\tau_{1}}, \frac{Q_{1}}{\theta}\right\} + e_{2} \min\left\{1, \frac{1}{\tau_{2}}, \frac{Q_{2}}{\theta}\right\}\right] < 0.$$

Since our solution is positive and bounded (see theorem 1) and $\xi_1 + \xi_2 + d > e_1 \min\left\{1, \frac{1}{\tau_1}, \frac{Q_1}{\theta}\right\} + e_2 \min\left\{1, \frac{1}{\tau_2}, \frac{Q_2}{\theta}\right\}$, we have y' < 0, that implies $\lim_{t \to \infty} y(t) = 0.$

The proof of Theorem 4 is given below.

Proof Since our solution is positive and bounded (see theorem 1), we get

$$\lim_{t\to\infty}\sup x_i(t)=K_i.$$

For sufficiently large t, we have

$$\frac{dy}{dt} = y \left[\frac{e_1 \mu \xi_1 x_1 + e_2 \mu \xi_2 x_2}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} - (\xi_1 + \xi_2 + d) \right] < \bar{\delta}y,$$

since $\bar{\delta} = \max_{(x_1, x_2) \in [0, k_1] \times [0, k_2]} = \left[\frac{e_1 \mu \xi_1 x_1 + e_2 \mu \xi_2 x_2}{1 + \mu \xi_1 \tau_1 x_1 + \mu \xi_2 \tau_2 x_2} - (\xi_1 + \xi_2 + d)\right]$. Now, since $\bar{\delta} < 0$, that implies

$$\lim_{t \to \infty} y(t) = 0.$$

Appendix A.3 Extra figures for the base model

See Fig. 15.





Fig. 15 Dynamics of the base model (5) under different light-dependent carrying capacity (K_1) of Phytoplankton (x_1) for $\alpha = 1.2$ (Non-homogeneous nutrient level)

Appendix B Foraging model analysis

Appendix B.1 Boundedness and positivity

The proof of boundedness and positive invariance of the foraging model (7) is given below.

Theorem 5 Solutions with initial conditions for (7) in the set

$$\Omega = \{(x_1, x_2, y) : 0 < x_1 < k_1, 0 < x_2 < k_2, 0 < y < P/\theta, q_1x_1 + q_2x_2 + \theta y < P\}$$

will remain in Ω for all forward time, where $k_i = \min\{K_i, \frac{P}{q_i}\}, i = 1, 2$.

Proof We will prove the theorem by contradiction. Suppose that the solution to the model S(t) starts inside our region and there exists some t_1 such that $S(t_1) \in \partial \Omega$, then it must either stay on the boundary or turn back into the interior of Ω . To consider the following cases using $\hat{y} = \max_{t \in [0, t_1]} y(t) < \frac{P}{\theta}$, $\hat{x}_1 = \max_{t \in [0, t_1]} x_1(t) < \min\{K_1, \frac{P}{q_1}\}$, and $\hat{x}_2 = \max_{t \in [0, t_1]} x_2(t) < \min\{K_2, \frac{P}{q_2}\}$. **Cases 1** $x_1(t_1) = 0$. Define $f(x_1) = \frac{\mu\xi_1(Q_1)x_1}{1 + \mu\xi_1(Q_1)\tau_1x_1 + \mu\xi_2(Q_2)\tau_2\hat{x}_2}$ and let $\hat{f} = f'(0) = \lim_{x_1 \to 0} = \frac{f(x_1)}{x_1}$. Then we have $\frac{dx_1}{dt} = r_1x_1 \min\left[1 - \frac{x_1}{K_1}, 1 - \frac{q_1}{Q_1}\right] - \frac{\mu\xi_1(Q_1)x_1y}{1 + \mu\xi_1(Q_1)\tau_1x_1 + \mu\xi_2(Q_2)\tau_2x_2}$ $\geq r_1x_1 \min\left[1 - \frac{x_1}{K_1}, 1 - \frac{q_1}{Q_1}\right] - \frac{\mu\xi_1(Q_1)x_1\hat{y}}{1 + \mu\xi_1(Q_1)\tau_1x_1 + \mu\xi_2(Q_2)\tau_2\hat{x}_2}$

which implies
$$x_1(t_1) \ge x_1(0) \exp^{-\phi t_1} > 0$$
, where ϕ is a constant. This contradicts $x_1(t_1) = 0$ and proves $S(t_1)$ does not reach this boundary.

Cases 2 $x_2(t_1) = 0$. Define $f(x_2) = \frac{\mu \xi_1(Q_1) x_2}{1 + \mu \xi_1(Q_1) \tau_1 \hat{x_1} + \mu \xi_2(Q_2) \tau_2 x_2}$ and let $\hat{f} = f'(0) = \lim_{x_2 \to 0} \frac{f(x_2)}{x_2}$. Then we have

$$\begin{aligned} \frac{dx_2}{dt} &= r_2 x_2 \min\left[1 - \frac{x_2}{K_2}, 1 - \frac{q_2}{Q_2}\right] - \frac{\mu \xi_2(Q_2) x_2 y}{1 + \mu \xi_1(Q_1) \tau_1 x_1 + \mu \xi_2(Q_2) \tau_2 x_2} \\ &\geq r_2 x_2 \min\left[1 - \frac{x_2}{K_2}, 1 - \frac{q_2}{Q_2}\right] - \frac{\mu \xi_2(Q_2) x_2 \hat{y}}{1 + \mu \xi_1(Q_1) \tau_1 \hat{x}_1 + \mu \xi_2(Q_2) \tau_2 x_2} \\ &\geq -\hat{f} x_2 \hat{y} = -\phi x_2, \end{aligned}$$

which implies $x_2(t_1) \ge x_2(0) \exp^{-\phi t_1} > 0$, where ϕ is a constant. This contradicts $x_2(t_1) = 0$ and proves $S(t_1)$ does not reach this boundary.

Case 3 $y(t_1) = 0$, note that $\forall t \in [0, t_1]$ we have

 $> -\hat{f}x_1\hat{y} = -\phi x_1,$

$$\frac{dy}{dt} = e_1 \min\left\{1, \frac{Q_1}{\theta}\right\} \frac{\mu \xi_1(Q_1) x_1 y}{1 + \mu \xi_1(Q_1) \tau_1 x_1 + \mu \xi_2(Q_2) \tau_2 x_2}$$

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$$+ e_{2} \min \left\{ 1, \frac{Q_{2}}{\theta} \right\} \frac{\mu \xi_{2}(Q_{2}) x_{2} y}{1 + \mu \xi_{1}(Q_{1}) \tau_{1} x_{1} + \mu \xi_{2}(Q_{2}) \tau_{2} x_{2}} \\ - \xi_{1} y - \xi_{2} y - d y \\ \geq -\xi_{1} y - \xi_{2} y - d y = -\alpha y,$$

which implies $y(t_1) \ge y(0) \exp^{-\alpha t_1} > 0$, where α is a constant. This contradicts $y(t_1) = 0$ and proves $S(t_1)$ does not reach this boundary.

Cases 4

At $t = t_1$, we have $q_1x_1(t_1) + q_2x_2(t_1) + \theta y(t_1) = P$, we can consider

$$r_1 x_1(t_1) \left[1 - \frac{x_1(t_1)}{\min\{K_1, \frac{P - x_2 Q_2 - \theta y}{q_1}\}} \right] \le r_1 x_1(t_1) \left[1 - \frac{x_1(t_1)}{\frac{P - x_2 q_2 - \theta y}{q_1}} \right] = 0,$$

similarly,

$$r_{2}x_{2}(t_{1})\left[1-\frac{x_{2}(t_{1})}{\min\{K_{2},\frac{P-x_{1}Q_{1}-\theta y}{q_{2}}\}}\right] \leq r_{2}x_{2}(t_{1})\left[1-\frac{x_{2}(t_{1})}{\frac{P-x_{1}q_{1}-\theta y}{q_{2}}}\right] = 0,$$

we have $0 < e_1, e_2 < 1$, and $\min(\theta, q_i) \le q_i < 1$, that gives

$$\begin{aligned} \frac{d(q_1x_1 + q_2x_2 + \theta y)}{dt}|_{t=t_1} \\ &= q_1x'_1 + q_2x'_2 + \theta y'|_{t=t_1} \\ &= e_1 \left[\min\left\{\theta, q_1\right\} - 1\right] \frac{\mu\xi_1(Q_1)x_1y}{1 + \mu\xi_1(Q_1)\tau_1x_1 + \mu\xi_2(Q_2)\tau_2x_2} \\ &+ e_2 \left[\min\left\{\theta, q_2\right\} - 1\right] \frac{\mu\xi_2(Q_2)x_2y}{1 + \mu\xi_1(Q_1)\tau_1x_1 + \mu\xi_2(Q_2)\tau_2x_2} - \theta(\xi_1 + \xi_2 + d)y \le 0. \end{aligned}$$

Therefore, $S(t_1)$ cannot cross this boundary.

Cases 5

 $x_1(t_1) = k_1 = \min\{K_1, \frac{p}{g_1}\}$. Since the phosphorus in the Phytoplankton cannot exceed the total phosphorus in the system we must have

$$x_1Q_1 \leq P$$
.

That gives

$$\frac{dx_1}{dt} = r_1 x_1 \min\left[1 - \frac{x_1}{K_1}, 1 - \frac{q_1}{Q_1}\right] - \frac{\mu \xi_1(Q_1) x_1 y}{1 + \mu \xi_1(Q_1) \tau_1 x_1 + \mu \xi_2(Q_2) \tau_2 x_2}$$

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$$\leq r_1 x_1 \left[1 - \frac{x_1}{\min\{K_1, \frac{x_1 Q_1}{q_1}\}} \right]$$
$$\leq r_1 x_1 \left[1 - \frac{x_1}{\min\{K_1, \frac{P}{q_1}\}} \right].$$

-

By standard comparison argument, $x_1(t_1) = k_1$, therefore S(t) cannot cross the boundary $x_1 = k_1$. A similar type of argument can be used for the case $x_2(t_1) = k_2 = \min\{K_2, \frac{P}{q_2}\}$.

All possibilities that $S(t_1)$ touches or crosses the boundary of Ω are excluded. Therefore, the Ω set is positive invariant for System (7). We thus claim that each solution of System (7) with initial condition $S(0) \in \Omega$ stays in Ω for any $t \ge 0$. \Box

Appendix B.2 Dynamics of the foraging model

To find the dynamics of the foraging model, we rewrite the foraging model in the following form:

$$\frac{dx_1}{dt} = x_1 F(x_1, x_2, y), \quad \frac{dx_2}{dt} = x_2 G(x_1, x_2, y), \quad \frac{dy}{dt} = y H(x_1, x_2, y),$$

where

$$\begin{split} F(x_1, x_2, y) &= \begin{cases} r_1 \left[1 - \frac{x_1}{K_1} \right] - \mu \xi_1(\mathcal{Q}_1) y \Delta(x_1, x_2, y), & \text{if } 1 - \frac{x_1}{K_1} \leq 1 - \frac{q_1}{\mathcal{Q}_1}; \\ r_1 \left[1 - \frac{q_1}{\mathcal{Q}_1} \right] - \mu \xi_1(\mathcal{Q}_1) y \Delta(x_1, x_2, y), & \text{if } 1 - \frac{x_1}{K_1} > 1 - \frac{q_1}{\mathcal{Q}_1}; \\ G(x_1, x_2, y) &= \begin{cases} r_2 \left[1 - \frac{x_2}{K_2} \right] - \mu \xi_2(\mathcal{Q}_2) y \Delta(x_1, x_2, y), & \text{if } 1 - \frac{x_2}{K_2} \leq 1 - \frac{q_2}{\mathcal{Q}_2}; \\ r_2 \left[1 - \frac{q_2}{\mathcal{Q}_2} \right] - \mu \xi_2(\mathcal{Q}_2) y \Delta(x_1, x_2, y), & \text{if } 1 - \frac{x_2}{K_2} > 1 - \frac{q_2}{\mathcal{Q}_2}; \\ r_2 \left[1 - \frac{q_2}{\mathcal{Q}_2} \right] - \mu \xi_2(\mathcal{Q}_2) y \Delta(x_1, x_2, y) - \xi_1(\mathcal{Q}_1) - \xi_2(\mathcal{Q}_2) - d, \\ & \text{if } 1 \leq \frac{\mathcal{Q}_1}{\theta} \text{ and } 1 \leq \frac{\mathcal{Q}_2}{\theta}; \\ (e_1 \mu \xi_1(\mathcal{Q}_1) x_1 + e_2 \frac{\mathcal{Q}_2}{\theta} \mu \xi_2(\mathcal{Q}_2) x_2) \Delta(x_1, x_2, y) - \xi_1(\mathcal{Q}_1) - \xi_2(\mathcal{Q}_2) - d, \\ & \text{if } 1 \leq \frac{\mathcal{Q}_1}{\theta} \text{ and } 1 \leq \frac{\mathcal{Q}_2}{\theta}; \\ (e_1 \frac{\mathcal{Q}_1}{\theta} \mu \xi_1(\mathcal{Q}_1) x_1 + e_2 \mu \xi_2(\mathcal{Q}_2) x_2) \Delta(x_1, x_2, y) - \xi_1(\mathcal{Q}_1) - \xi_2(\mathcal{Q}_2) - d, \\ & \text{if } 1 \leq \frac{\mathcal{Q}_1}{\theta} \text{ and } 1 \leq \frac{\mathcal{Q}_2}{\theta}; \\ (e_1 \frac{\mathcal{Q}_1}{\theta} \mu \xi_1(\mathcal{Q}_1) x_1 + e_2 \frac{\mathcal{Q}_2}{\theta} \mu \xi_2(\mathcal{Q}_2) x_2) \Delta(x_1, x_2, y) - \xi_1(\mathcal{Q}_1) - \xi_2(\mathcal{Q}_2) - d, \\ & \text{if } 1 > \frac{\mathcal{Q}_1}{\theta} \text{ and } 1 \leq \frac{\mathcal{Q}_2}{\theta}; \\ (e_1 \frac{\mathcal{Q}_1}{\theta} \mu \xi_1(\mathcal{Q}_1) x_1 + e_2 \frac{\mathcal{Q}_2}{\theta} \mu \xi_2(\mathcal{Q}_2) x_2) \Delta(x_1, x_2, y) - \xi_1(\mathcal{Q}_1) - \xi_2(\mathcal{Q}_2) - d, \\ & \text{if } 1 > \frac{\mathcal{Q}_1}{\theta} \text{ and } 1 \leq \frac{\mathcal{Q}_2}{\theta}; \end{cases} \end{split}$$

where $\Delta(x_1, x_2, y) = (1 + \mu \xi_1(Q_1)\tau_1 x_1 + \mu \xi_2(Q_2)\tau_2 x_2)^{-1}$.

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To determine the local stability of these equilibria, we calculate the Jacobian matrix of the above model

$$J(x_1, x_2, y) = \begin{pmatrix} F + x_1 F_{x_1}(x_1, x_2, y) & x_1 F_{x_2}(x_1, x_2, y) & x_1 F_y(x_1, x_2, y) \\ x_2 G_{x_1}(x_1, x_2, y) & G + x_2 G_{x_2}(x_1, x_2, y) & x_2 G_y(x_1, x_2, y) \\ y H_{x_1}(x_1, x_2, y) & y H_{x_2}(x_1, x_2, y) & H + y H_y(x_1, x_2, y) \end{pmatrix}.$$

$$\begin{split} F_{x_1} &= \begin{cases} -\frac{r_1}{K_1} - \mu y(\xi_1(Q_1)\Delta)_{x_1}, & \text{if } 1 - \frac{x_1}{K_1} \leq 1 - \frac{q_1}{Q_1}; \\ -r_1\left(\frac{q_1}{Q_1}\right)_{x_1} - \mu y(\xi_1(Q_1)\Delta)_{x_1}, & \text{if } 1 - \frac{x_1}{K_1} > 1 - \frac{q_1}{Q_1}; \end{cases} \\ F_{x_2} &= \begin{cases} -\mu y(\xi_1(Q_1)\Delta)_{x_2}, & \text{if } 1 - \frac{x_1}{K_1} \leq 1 - \frac{q_1}{Q_1}; \\ -r_1\left(\frac{q_1}{Q_1}\right)_{x_2} - \mu y(\xi_1(Q_1)\Delta)_{x_2}, & \text{if } 1 - \frac{x_1}{K_1} > 1 - \frac{q_1}{Q_1}; \end{cases} \\ F_y &= \begin{cases} -\mu (y\xi_1(Q_1)\Delta)_y, & \text{if } 1 - \frac{x_1}{K_1} \leq 1 - \frac{q_1}{Q_1}; \\ -r_1\left(\frac{q_1}{Q_1}\right)_y - -\mu (y\xi_1(Q_1)\Delta)_y, & \text{if } 1 - \frac{x_1}{K_1} > 1 - \frac{q_1}{Q_1}; \end{cases} \\ G_{x_1} &= \begin{cases} -\mu y(\xi_2(Q_2)\Delta)_{x_1}, & \text{if } 1 - \frac{x_2}{K_2} \leq 1 - \frac{q_2}{Q_2}; \\ -r_2\left(\frac{q_2}{Q_2}\right)_{x_1} - \mu y(\xi_2(Q_2)\Delta)_{x_1}, & \text{if } 1 - \frac{x_2}{K_2} > 1 - \frac{q_2}{Q_2}; \end{cases} \\ G_y &= \begin{cases} -\mu (y\xi_2(Q_2)\Delta)_y, & \text{if } 1 - \frac{x_2}{K_2} \leq 1 - \frac{q_2}{Q_2}; \\ -r_2\left(\frac{q_2}{Q_2}\right)_{x_2} - -\mu y(\xi_2(Q_2)\Delta)_{x_2}, & \text{if } 1 - \frac{x_2}{K_2} > 1 - \frac{q_2}{Q_2}; \end{cases} \\ G_y &= \begin{cases} -\mu (y\xi_2(Q_2)\Delta)_y, & \text{if } 1 - \frac{x_2}{K_2} \leq 1 - \frac{q_2}{Q_2}; \\ -r_2\left(\frac{q_2}{Q_2}\right)_y - -\mu (y\xi_2(Q_2)\Delta)_y, & \text{if } 1 - \frac{x_2}{K_2} > 1 - \frac{q_2}{Q_2}; \end{cases} \\ \end{array}$$

$$\begin{pmatrix} \frac{q_1}{Q1} \end{pmatrix}_{x_1} = \frac{q_1}{P - \theta y}, \ \begin{pmatrix} \frac{q_1}{Q1} \end{pmatrix}_{x_2} = \frac{q_1}{\alpha (P - \theta y)}, \ \begin{pmatrix} \frac{q_2}{Q2} \end{pmatrix}_{x_1} = \frac{q_2 \alpha}{P - \theta y}, \ \begin{pmatrix} \frac{q_2}{Q2} \end{pmatrix}_{x_2} = \frac{q_2}{P - \theta y}.$$

Theorem 6 Let us denote four consumer-free equilibria as (i) $E_{000} = (0, 0, 0)$, (ii) $E_{100} = (k_1, 0, 0)$, (iii) $E_{010} = (0, k_2, 0)$, and (iv) $E_{110} = (k_1, k_2, 0)$. The (i)-

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(iii) consumer-free equilibria are unstable but the $E_{110} = (k_1, k_2, 0)$ is stable if $H(k_1, k_2, 0) < 0$.

Proof At the E_{000} , the Jacobian matrix takes the form

$$J(E_{000}) = \begin{pmatrix} r_1 & 0 & 0 \\ 0 & r_2 & 0 \\ 0 & 0 & - \end{pmatrix}.$$

The eigenvalues come with a different sign. That gives E_0 is always unstable. This implies that a complete collapse of the system is impossible.

At E_{100} , the Jacobian matrix is

$$J(E_{100}) = \begin{pmatrix} k_1 F_{x_1}(k_1, 0, 0) \ k_1 F_{x_2}(k_1, 0, 0) \ k_1 F_{y}(k_1, 0, 0) \\ 0 \ G(k_1, 0, 0) \ 0 \\ 0 \ H(k_1, 0, 0) \end{pmatrix}$$
$$= \begin{pmatrix} -* & * \\ 0 \ r_2 \ 0 \\ 0 \ 0 \ H(k_1, 0, 0) \end{pmatrix}.$$

The eigenvalues come with a different sign, which does not matter on the sign of $H(k_1, 0, 0)$. That gives E_{100} unstable as well.

At E_{010} , the Jacobian matrix is

$$J(E_{010}) = \begin{pmatrix} F(0, k_2, 0) & 0 & 0 \\ k_2 G_{x_1}(0, k_2, 0) & k_2 G_{x_2}(0, k_2, 0) & k_2 G_y(0, k_2, 0) \\ 0 & 0 & H(0, k_2, 0) \end{pmatrix}$$
$$= \begin{pmatrix} r_1 & 0 & 0 \\ * & - & * \\ 0 & 0 & H(0, k_2, 0) \end{pmatrix}.$$

We get E_{010} is unstable.

At E_{110} , biologically the ratio between total phosphorus and minimum P:C ratio $\left(\frac{P}{q_I}\right)$ is way too high than the carrying capacity (K_i) . That gives $k_1 = \min\{K_1, \frac{P}{q_1}\} =$

 K_1 and $k_2 = \min\{K_2, \frac{P}{q_2}\} = K_2$ and equilibria become $E_{110} = (K_1, K_2, 0)$. Then the Jacobian matrix becomes

$$J(E_{110}) = \begin{pmatrix} k_1 F_{x_1}(k_1, k_2, 0) & k_1 F_{x_2}(k_1, k_2, 0) & k_1 F_y(k_1, k_2, 0) \\ k_2 G_{x_1}(k_1, k_2, 0) & k_2 G_{x_2}(k_1, k_2, 0) & k_2 G_y(k_1, k_2, 0) \\ 0 & 0 & H(k_1, k_2, 0) \end{pmatrix}$$
$$= \begin{pmatrix} -0 & * \\ 0 - & * \\ 0 & 0 & H(k_1, k_2, 0) \end{pmatrix}.$$

The stability of $E_{110} = (K_1, K_2, 0)$ depends on the condition of $H(k_1, k_2, 0) < 0$. \Box

Appendix B.3 Interior equilibria

Interior equilibria for the foraging model under nutrient value P:

- Case 1: $P \ge 0.03$ (Favorable Habitat)
- Case 2: 0.02 < P < 0.03 (Ecotone)
- Case 3: $P \le 0.02$ (Unfavorable Habitat)

See Fig. 16, 17 and 18.







Fig. 17 For P = 0.025, $K_1 = 1.75$, $K_2 = 1.8$, and $\theta = 0.03$



Fig. 18 For P = 0.015, $K_1 = 1.75$, $K_2 = 1.8$, and $\theta = 0.03$

Appendix B.4 Extra figures for the foraging model

See Fig. 19.



Fig. 19 Dynamics of the foraging model (7) under different light-dependent carrying capacity (K_1) of Phytoplankton (x_1) for $\alpha = 1.2$ (Non-homogeneous nutrient level)

Acknowledgements Hao Wang's research was partially supported by the Natural Sciences and Engineering Research Council of Canada (Discovery Grant RGPIN-2020-03911 and NSERC Accelerator Grant RGPAS-2020-00090) and the Canada Research Chairs Program (Tier 1 Canada Research Chair Award).

Data availability Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare that they have no Conflict of interest. All authors satisfy ethical responsibilities.

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